



THE INFLUENCE OF TEMPERATURE AND BREEDING UPON THE RATE OF GROWTH OF CHICK EMBRYOS

BY

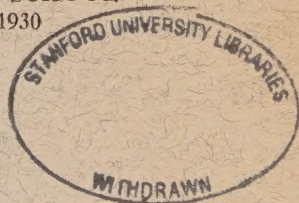
L. C.

EARL WILTON HENDERSON

B. S. in Agr., University of Missouri, 1921
A. M., University of Missouri, 1924

THESIS

SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIRE-
MENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY IN
ANIMAL HUSBANDRY IN THE GRADUATE SCHOOL
OF THE UNIVERSITY OF ILLINOIS, 1930



Reprinted from the UNIVERSITY OF MISSOURI AGRICULTURAL EXPERIMENT STATION
RESEARCH BULLETIN 149, SEPTEMBER, 1930.

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UNIVERSITY OF MISSOURI

COLLEGE OF AGRICULTURE

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RESEARCH BULLETIN 149

GROWTH AND DEVELOPMENT

With Special Reference to Domestic Animals

XVI. The Influence of Temperature and Breeding Upon the Rate of Growth of Chick Embryos

(Publication authorized August 27, 1930)



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SEPTEMBER, 1930

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GROWTH AND DEVELOPMENT

With Special Reference to Domestic Animals

XVI. The Influence of Temperature and Breeding upon the Rate of Growth of Chick Embryos.

EARL WILTON HENDERSON

OBJECT AND METHODS

Object of Investigation

The objects of this investigation were: (1) To determine the rate of growth of the chick embryo as measured by wet and dry weight and nitrogen content at the optimum, minimum, and maximum temperatures; (2) to verify the limits of temperature for embryonic development to the normal ninety-six hour stage; (3) to study the influence of breeds of parent stock upon embryonic development under normal conditions.

Method

For the study of the limits of temperature on development, 150 to 200 eggs from Single Comb White Leghorn hens under uniform management conditions were incubated at three temperatures, (1) 96°F. (2) 101.8 F. and (3) 107°F. Humidity and ventilation conditions were maintained as uniform as possible. Eggs were turned twice daily. This phase of the investigation was done at the University of Missouri between April 1 and June 15, 1927.

For the study of the influence of breed of parent stock upon embryonic development, eggs from the following classes of breeding stock at the University of Illinois were used: (1) Dark Cornish, (2) Single Comb White Leghorn, (3) Dark Cornish hens mated to Single Comb White Leghorn males, (4) White Leghorn hens mated to Dark Cornish Males. This phase of the work was done at the University of Illinois between January and July, 1928.

In the study of the influence of breed of parent stock the temperature selected was 101.8°F. primarily because this temperature was used by Murray (1925) and regarded as standard by Needham (1926), although the work of Philips and Brooks (1923) and others indicates that 101°F. is the optimum temperature for hot air incubators of the type used in the study of temperature influences. The incubator used in the study of temperature influences was a hot air type, 150 egg size, operated in

a room at approximately 70°F. In the study of breed influences, the incubator used was a 200 egg size, single tray type, with a "mat" type electric heating element fitted in the top of the egg chamber.

The following records were kept: (1) Number of eggs set, (2) initial weight of ten representative eggs, (3) temperatures and per cent relative humidity in the egg chamber, (4) number of eggs infertile, (5) weights of ten representative eggs at intervals of six days, to determine loss in weight from evaporation.

The rate of growth was determined by extracting duplicate samples of from four to six embryos daily, beginning when the embryos had reached approximately the normal ninety-six hour stage. The method of extraction was to allow the eggs to be extracted to rest for fifteen to twenty minutes on the small end after which time the shell was broken over the air cell, shell and shell membranes were removed and the embryo extracted by seizing the yolk stalk with a pair of forceps. The amnion was punctured with shears and the amniotic fluid was drained out and all extra embryonic membranes visible to the eye were removed with shears.

Immediately after extraction, the embryos were dropped into covered, tared, crucibles and weighed on a balance sensitive to .1 mg. after which the embryos were dried to constant weight in an oven at 96° to 98°C. The dried residue was covered with concentrated sulphuric acid, transferred to a Kjeldahl flask and nitrogen was determined by the Kjeldahl method. The tabulated data include the following: Average wet and dry weights, and nitrogen content per embryo for periods of incubation from the 4th to the 20th day.

METHODS OF PRESENTING DATA

The data obtained in this investigation are presented first in tabular form. Table 1 shows results obtained at a temperature of 96°F., Table 2 shows results at 101.8°F., and Table 3 results at 107°F. Table 4 is a consolidation of all the dry weights. It includes the calculated dry weights at temperatures of 99°F. and 105°F. estimated from wet weight data of Henderson (1924). Table 5 shows the data from pure bred Cornish from the University of Illinois flock. Table 6 shows similar data from pure bred Single Comb White Leghorns from the same station. Table 7 shows the results obtained from embryos produced by mating Dark Cornish males to Single Comb White Leghorn females. Table 8 shows results obtained from embryos produced by the reciprocal of the above mating. Table 9 is composed of wet weights from University of Missouri Single Comb White Leghorns. Table 10 shows results obtained from all embryos incubated at 101.8°F. (38.8°C.).

TABLE 1.—UNIVERSITY OF MISSOURI S. C. W. L. CHICK EMBRYOS INCUBATED AT 96 DEGREES F. RELATIVE HUMIDITY 59.5%. DRIED AT 96 DEGREES C.

Age of embryo Days	Av. wt. of nitrogen in one embryo gms.	Percent nitrogen	Av. wt. of protein in one embryo gms.	Percent protein (Nx6.25)	Av. wt. of one dry embryo gms.	Av. wt. of one wet embryo gms.	Av. wt. of H ₂ O in one embryo gms.	Percent moisture
8	.0017	10.49	.0107	65.56	.0163	.3134	.2971	95.3
9	.0030	10.93	.0189	68.31	.0277	.5246	.4969	94.7
10	.0052	10.40	.0322	65.00	.0495	.8693	.8198	94.3
12	.0100	10.73	.0623	67.06	.0929	1.5623	1.4694	94.0
14	.0126	10.69	.0786	66.81	.1569	2.5816	2.4247	93.9
16	.0244	12.61	.1527	78.81	.3683	5.1552	4.7869	92.9
18	.0693	10.94	.4331	68.37	.6329	7.6114	6.9785	91.6
20	.1364	10.90	.8526	68.12	1.2511	11.6309	10.3798	89.3

TABLE 2.—UNIVERSITY OF MISSOURI S. C. W. L. CHICK EMBRYOS INCUBATED AT 101.8 DEGREES F. RELATIVE HUMIDITY 62%. DRIED AT 96 DEGREES C.

Age of embryo- o Days	Av. wt. of ni- trogen in one embryo gms.	Percent nitrogen	Av. wt. of pro- tein in one em- bryo gms.	Percent protein (Nx6.25)	Av. wt. of one dry embryo gms.	Av. wt. of one wet embryo gms.	Av. wt. of H ₂ O in one embryo gms.	Percent moisture
4	.0003	9.59	.0021	59.812	.0034	.0656	.0622	94.81
5	.0010	9.59	.0065	59.98	.0108	.203	.1922	94.68
6	.0023	9.67	.0110	60.43	.0239	.4417	.4178	94.63
7	.0042	9.67	.0261	60.49	.0431	.7602	.7171	94.33
8	.0087	10.58	.0546	66.12	.0826	1.3477	1.2651	93.90
9	.0119	10.14	.0744	63.35	.1175	1.8470	1.7295	93.60
10	.0201	10.92	.1256	68.30	.1839	2.6708	2.4860	93.12
11	.0314	11.16	.1961	69.78	.2810	3.7303	3.4493	92.90
12	.0501	11.08	.3132	69.29	.4519	5.5533	5.1014	91.90
13	.0708	10.84	.4424	67.74	.6530	7.1474	6.4944	90.80
14	.1370	11.57	.8561	72.30	1.1839	8.8553	7.6714	86.67
15	.2309	11.66	1.4432	72.87	1.9803	13.3434	11.3631	85.20
16	.3325	11.48	2.0779	71.64	2.9004	16.6058	13.7054	82.60
17	.3859	11.08	2.4119	69.31	3.7345	20.8031	17.0686	81.70
18	.4105	10.28	2.5656	64.29	3.9904	22.5553	18.5649	82.3
19	.4991	9.32	3.1192	59.28	5.2619	28.8203	23.5584	81.6
20	.5185	8.72	3.2405	54.52	5.9432	28.6532	22.7106	79.3

TABLE 3.—S. C. W. L. CHICK EMBRYOS INCUBATED AT 107 DEGREES F. RELATIVE HUMIDITY 61.4%. DRIED AT 96 DEGREES C.

Age of embryo— Days	Average wt. of ni- trogen in one embryo gms.	Percent nitrogen	Average wt. of pro- tein in one em- bryo gms.	Percent protein dry (Nx6.25)	Average wt. of one dry embryo gms.	Average wt. of H ₂ O wet embryo gms.	Average wt. of H ₂ O in one embryo gms.	Percent moisture
4	.0006	10.87	.0035	67.9	.0052	.0961	.0909	94.6
6	.0036	10.73	.0224	67.06	.0334	.6529	.6195	94.9
8	.0104	10.69	.0650	66.81	.0966	1.6091	1.5125	94.
10	.0214	10.41	.1339	65.06	.2055	2.9898	2.7843	92.9
12	.0600	10.50	.3749	65.62	.5708	6.6143	6.0435	91.5
14	.1554	11.05	.9714	69.06	1.2299	10.2785	9.0486	88.0
16	.2507	10.32	1.5667	64.5	2.4282	15.6434	13.2152	84.5
18	.2064	8.18	1.2897	53.68	2.5204	15.1821	12.6617	83.5

TABLE 4.—DRY WEIGHTS OF UNIVERSITY OF MISSOURI S. C. W. L. CHICK EMBRYOS INCUBATED AT VARIOUS TEMPERATURES

Age in days	Temperatures—96° F. Weights----- (gms.)	99° F. gms.	101.8° F. (gms.)	105° F. (gms.)	107° F. (gms.)
4			.0034	.0122	.0052
5		.0031	.0108	.0234	
6		.0101	.0239	.0464	.0334
7		.0214	.0431	.0702	
8	.0163	.0389	.0826	.1219	.0956
9	.0277	.0789	.1175	.1828	
10	.0495	.1095	.1839	.2920	.2055
11		.1514	.2810	.4444	
12	.0929	.2496	.4519	.7188	.5708
13		.3949	.6530	.8862	
14	.1569	.8214	.1839	1.6182	1.2299
15		1.2062	1.9803	1.8380	
16	.3683	1.9121	2.9004	2.8683	2.4282
17		2.3214	3.7345	3.1662	
18	.6329	2.8134	3.9904		2.5204
19		3.2253	5.2619		
20		4.4935	5.9432		
21	1.2511	5.6165			

TABLE 5.—DARK CORNISH CHICK EMBRYOS (III.) INCUBATED AT 101.8°F. AVERAGE RELATIVE HUMIDITY 71.6%. DRIED AT 98°C.

Age of embryo- Days	Av. wt. of ni- trogen in one embryo gms.	Percent nitrogen	Av. wt. of pro- tein in one em- bryo gms.	Percent protein (Nx6.25)	Av. wt. of one dry embryo gms.	Av. wt. of one wet embryo gms.	Av. wt. of H ₂ O in one embryo gms.	Percent moisture
4	.0003	9.80	.0020	61.25	.0033	.0618	.0584	94.5
5	.0011	10.42	.0068	65.12	.0104	.1877	.1773	94.5
6	.0024	10.74	.0152	67.12	.0226	.3989	.3763	94.4
7	.0052	10.40	.0325	65.00	.0500	.8459	.7958	94.1
8	.0060	10.18	.0431	63.62	.0677	1.1257	1.0580	93.8
9	.0099	9.64	.0619	60.25	.1178	1.8312	1.7134	93.5
10	.0178	10.26	.1113	64.12	.1747	2.6196	2.4449	93.4
11	.0270	10.72	.1684	67.00	.2512	3.4366	3.1854	92.7
12	.0417	9.98	.2608	62.37	.4180	5.1575	4.7395	92.0
13	.0681	10.60	.4256	66.25	.6421	7.0143	6.3722	90.9
14	.1566	11.21	.9790	70.06	1.3972	11.3240	9.9268	87.7
15	.2248	11.12	1.4049	69.50	1.9704	13.8304	11.8600	85.8
16	.3073	11.18	1.9203	69.87	2.7459	16.7473	14.0014	83.7
17	.3440	10.96	2.1992	68.50	3.1377	19.2820	16.1443	83.7
18	.4112	10.48	2.5700	65.60	3.9218	22.8911	18.9695	83.0
19	.6148	9.35	3.8425	58.43	6.5715	32.4550	25.8835	79.7
20	.7226	7.91	4.5083	49.43	9.1321	36.1328	27.0007	79.9

TABLE 6.—UNIVERSITY OF ILLINOIS S. C. W. L. CHICK EMBRYOS INCUBATED AT 101.3 DEGREES F. RELATIVE HUMIDITY 71.6%. DRIED AT 96 DEGREES C.

Age of embryo- o Days	Av. wt. of ni- trogen in one embryo gms.	Percent nitrogen	Av. wt. of pro- tein in one em- bryo (gms.)	Percent protein (Nx6.25)	Av. wt. of one dry embryo gms.	Av. wt. of one wet embryo gms.	Av. wt. of H ₂ O in one embryo gms.	Percent moisture
4	.0003	8.06	.0019	50.37	.0038	.0748	.0709	94.8
5	.0010	9.38	.0064	58.60	.0110	.2077	.1967	94.3
6	.0030	10.79	.0188	67.43	.0278	.4985	.4707	94.2
7	.0050	11.00	.0313	68.75	.0455	.7694	.7240	94.2
8	.0073	10.49	.0457	65.56	.714	1.1638	1.0925	94.0
9	.0117	10.37	.0729	64.81	.1124	1.7508	1.6384	93.2
10	.0170	10.26	.1125	64.12	.1739	2.5399	2.3660	93.2
11	.0304	10.54	.1903	65.87	.2880	3.8307	3.5427	92.5
12	.0430	10.48	.2685	65.50	.4096	5.7237	5.3141	92.7
13	.0846	10.91	.5288	68.18	.7748	9.4603	8.6854	91.8
14	.1522	11.19	.9514	69.93	1.3595	10.7243	9.3648	87.3
15	.1870	11.02	1.1686	68.87	1.6952	11.7508	10.0556	85.6
16	.3376	11.13	2.1097	69.56	3.0304	17.4233	14.3929	82.6
17	.3696	10.35	2.3100	64.68	3.5699	20.8215	17.2516	82.8
18	.4130	10.05	2.5814	62.81	4.1060	23.7453	19.6393	82.7
19	.4634	9.69	2.8963	60.56	4.7813	25.6827	20.9014	81.5
20	.9540	9.05	5.9627	56.56	10.5337	41.1675	30.6337	79.5

TABLE 7.—UNIVERSITY OF ILLINOIS CHICK EMBRYOS FROM DARK CORNISH X S. C. W. L. INCUBATED AT 101.8 DEGREES F. RELATIVE HUMIDITY 74.8%. DRIED AT 98°C.

Age of embryo- o Days	Av. wt. of ni- trogen in one embryo gms.	Percent nitrogen	Av. wt. of pro- tein in one em- bryo gms.	Percent protein (Nx6.25)	Av. wt. of one dry embryo gms.	Av. wt. of one wet embryo gms.	Av. wt. of H ₂ O in one embryo gms.	Percent moisture
4	.0003	8.95	.0026	55.93	.0034	.0600	.0567	94.5
5	.0019	10.50	.0062	65.62	.0095	.1707	.1612	94.4
6	.0023	11.07	.0145	69.18	.0210	.3933	.3723	94.7
7	.0052	10.55	.0327	65.93	.0495	.8397	.7902	94.2
8	.0079	10.60	.0494	66.25	.0765	1.0606	.9861	93.0
9	.0106	10.72	.0663	67.00	.0989	1.5327	1.4338	93.5
10	.0169	9.05	.1057	56.56	.1866	2.7391	2.5525	93.3
11	.0294	10.58	.1836	66.12	.2775	3.7868	3.5093	92.7
12	.0485	11.02	.3032	68.87	.4401	5.3620	4.9220	91.7
13	.0956	11.27	.5978	70.43	.8475	7.9522	7.1047	90.0
14	.1301	10.69	.8134	66.81	1.2164	10.2379	9.0215	88.1
15	.2344	11.53	1.5898	72.06	2.2061	14.7474	12.5413	85.1
16	.3095	11.30	1.9322	70.62	2.7397	17.2154	14.4757	84.1
17	.3688	10.61	2.3047	66.31	3.4747	20.6702	17.1955	83.2
18	.5034	10.68	3.1475	66.75	4.9923	28.4934	23.5010	82.5
19	.5654	11.35	3.5334	70.93	4.9795	28.5442	23.5647	82.6
20	.9537	8.60	5.9606	53.75	10.0754	42.2242	32.1488	76.2

TABLE 8.—CHICK EMBRYOS FROM S. C. W. L. X DARK CORNISH INCUBATED AT 101.8°F. AVERAGE RELATIVE HUMIDITY 74.8%.
DRIED AT 98 DEGREES C.

Age of embryo Days	Av. wt. of nitrogen in one embryo gms.	Percent nitrogen	Av. wt. of protein in one embryo (gms.)	Percent protein (Nx6.25)	Av. wt. of one dry embryo (gms.)	Av. wt. of one wet embryo (gms)	Av. wt. of H ₂ O in one embryo (gms.)	Percent moisture
4	.0003	9.64	.0017	60.25	.0029	.0553	.0524	94.3
5	.0009	10.95	.0055	68.43	.0080	.1504	.1423	94.6
6	.0025	11.22	.0159	70.12	.0227	.4088	.3861	94.5
7	.0045	11.12	.0282	69.50	.0405	.7008	.6603	94.7
8	.0078	10.58	.0489	66.12	.0739	1.2177	1.1438	94.0
9	.0120	10.86	.0750	67.87	.1104	1.8113	1.7007	94.0
10	.0198	9.74	.1235	60.87	.2029	2.8511	2.6482	92.8
11	.0288	10.72	.1803	67.00	.2690	3.4448	3.1757	92.2
12	.0477	10.91	.2979	68.18	.4367	5.3501	4.9134	91.8
13	.0775	11.03	.4846	68.93	.7024	7.4684	6.7660	90.6
14	.1325	10.96	.8279	68.5	1.2079	9.7605	8.5526	87.6
15	.2620	11.85	1.6373	74.06	2.2100	14.3727	12.1627	84.6
16	.3386	11.58	2.1159	72.37	2.9214	17.1377	14.2180	83.0
17	.3889	11.27	2.4303	70.43	3.4500	20.5179	17.0679	83.2
18	.4193	10.39	2.6203	64.93	4.0351	22.9455	18.4104	80.3
19	.5370	8.14	3.3559	50.87	6.5903	27.7564	21.1661	76.3
20	.9750	9.49	6.0934	59.31	10.2705	40.7085	30.4380	74.9

TABLE 9.—AVERAGE DAILY WEIGHT IN GRAMS OF MISSOURI S. C. W. L. CHICK EMBRYOS AT VARIOUS TEMPERATURES

Age in days	Relative Humidity % Temperature	(34.44°C. (94°F.	35°C. 95°F.	59.5% 35.56°C. 96°F.	37.22°C. 99°F.	62% 38.77°C. 101.8°F.	40.56°C. 105°F.	61.4% 41.67°C. 107°F.
4					.059	.0656	.225	.0961
5					.189	.203	.434	
6					.377	.4417	.909	.6529
7					.639	.7602	1.376	
8			.311	.3134	1.234	1.3477	2.032	1.6091
9			.583	.5246	1.591	1.8470	3.046	
10		.475	.939	.8693	2.133	2.6708	4.113	2.9898
11			1.323		3.081	3.7303	6.259	
12		1.252	1.730	1.5623	4.292	5.5533	8.457	6.6143
13			2.226		6.162	7.1474	10.426	
14				2.5816	8.758	8.8553	13.485	10.2785
15			3.525	5.1552	10.989	13.3434	15.314	
16			5.150		12.685	16.6058	18.505	15.6434
17				7.6114	15.895	20.8031	20.427	
18			8.322		17.529	22.5553		15.1821
19				11.6309	21.708	28.8203		
20					27.133	28.6532		
21			11.49					

TABLE 10.—MEAN WEIGHT OF CHICK EMBRYOS INCUBATED AT 38.8°C. (101.8°F.)

Age in days	Number	Mean wet weight	Mean dry weight	Number	Mean weight of nitrogen
		<i>Grams</i>	<i>Grams</i>		<i>Grams</i>
4	47	.0626	.0033	47	.0003
5	36	.1882	.0101	36	.0010
6	31	.4329	.0239	31	.0025
7	34	.7805	.0454	28	.0050
8	33	1.1987	.0748	30	.0078
9	28	1.7723	.1125	25	.0115
10	28	2.6673	.1828	22	.0188
11	30	3.6421	.2735	30	.0295
12	28	5.4341	.4306	28	.0460
13	26	7.8236	.7161	26	.0781
14	26	10.2083	1.2823	26	.1432
15	22	13.5848	2.0095	20	.2324
16	20	16.9649	2.8836	20	.3273
17	18	20.4227	3.5048	15	.3684
18	14	23.6774	4.1466	14	.4255
19	12	28.6798	5.5744	12	.5297
20	12	36.2566	8.6497	12	.7737

In order to visualize results the tabulated data are presented in several graphical forms including arithmetical coordinate, logarithmic coordinate and arithlog charts. Cumulative growth is shown in some cases by curves on all three types of paper. Arithlog and coordinate logarithmic paper is used to show comparative growth under varying conditions and to fit mathematical formulae to the curves in some cases by the graphical method. Arithlog paper is especially useful in visualizing the relative percentage rates of growth of embryos under different conditions and also the relative growth of various substances in the chick embryo. This paper is also useful in determining the type of formula which will fit a particular curve. A curve, which can be represented by an exponential equation of the type $y = ae^{bx}$ will be a straight line when plotted on Arithlog paper.

Growth curves for a number of different organisms have been found by Brody (1927) to fit an exponential equation of the type $W = Ae^{kt}$ where W represents the weight, A is a constant having the value of W when t , age, is 0, $100k$ is the instantaneous percentage rate of growth, e is the base of natural logarithms. While this formula has been shown to fit growth curves of various organisms it will not fit the entire age curve of the chick embryo as has been demonstrated by Henderson and Brody (1927). While the entire growth curve of the chick embryo apparently cannot be represented by such an exponential formula, still this formula can be used to represent stages in the growth curve. Relatively large segments of the curve approximate a straight line when the data are plotted on arithlog paper. Of course, any curve may be represented by a series of straight lines if the lines are short enough, but there

must be significance in the fact that such relatively large segments of the curves here being considered approximate straight lines when thus plotted.

For this reason, it seems desirable to apply the formula $W = Ae^{kt}$ to age curves of the chick embryo, and thus to correlate the growth processes of the chick with those of other organisms.

The choice of a graph should depend upon the biological relationships one wishes to demonstrate. It is quite possible that biological significance can be lost if too much smoothing of data curves is attempted in order to fit them to empirical formulae. As far as growth in wet

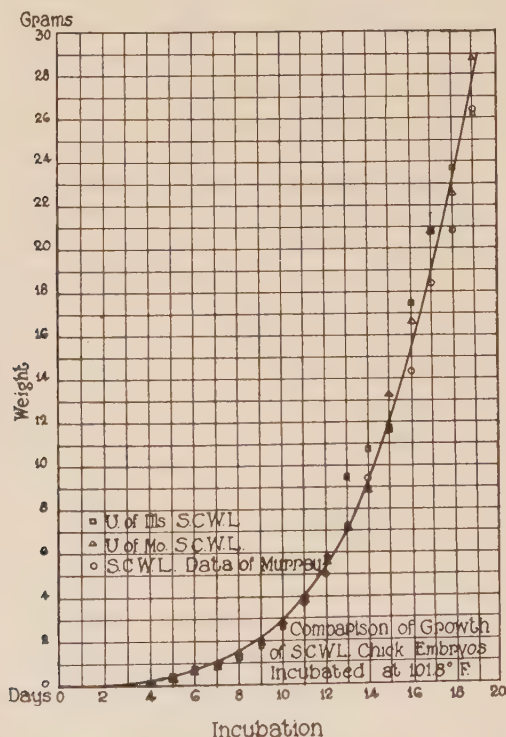


Fig. 1.—A comparison of the growth data of S. C. White Leghorn chick embryos.

weight is concerned, the formula of Murray $W = .668 t^{3.6}$ fits the data as a whole in a satisfactory manner, but with certain conspicuous deviations. The data points obtained in this investigation seem to agree fairly well with those of Murray, except for the older embryos as shown in Figs. 1 and 2. Even though the two sets of data were obtained

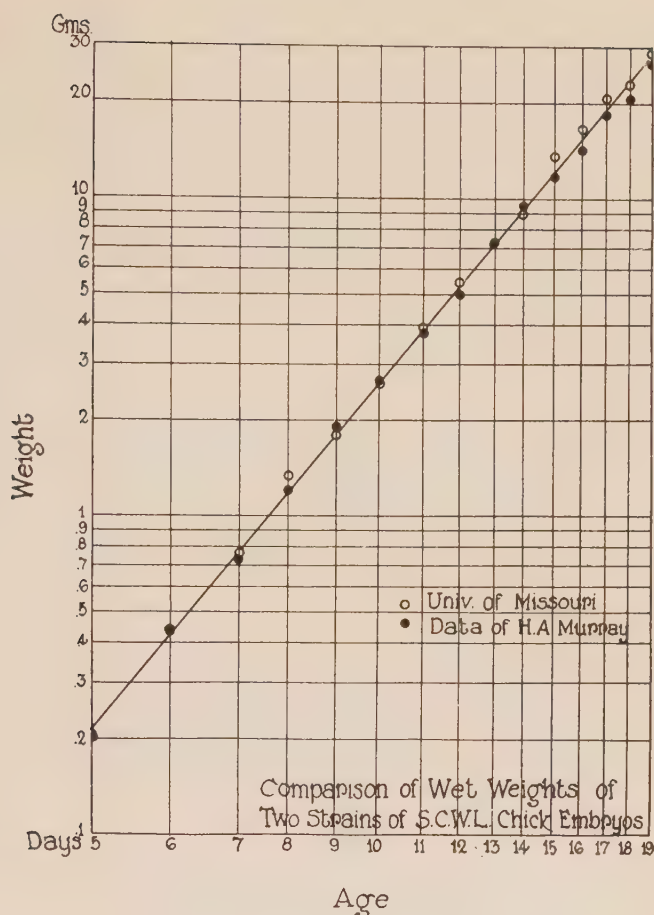


Fig. 2.—Murray's and Missouri data, wet weights, plotted on logarithmic coordinate paper.

by different technique the deviations from the straight line in Fig. 2 are in general in the same direction for both sets. This suggests that there are changes in the curves of possible biological significance that are not due entirely to experimental error. A comparison of the dry weight curve of the two investigations plotted on logarithmic paper still further emphasizes this point as shown in Figure 3. Though the goodness of fit of the curve for the data as a whole might be satisfactory for some statistical purposes, it may not be sufficiently good from a biological standpoint ignoring as it does certain conspicuous deviations. Charts

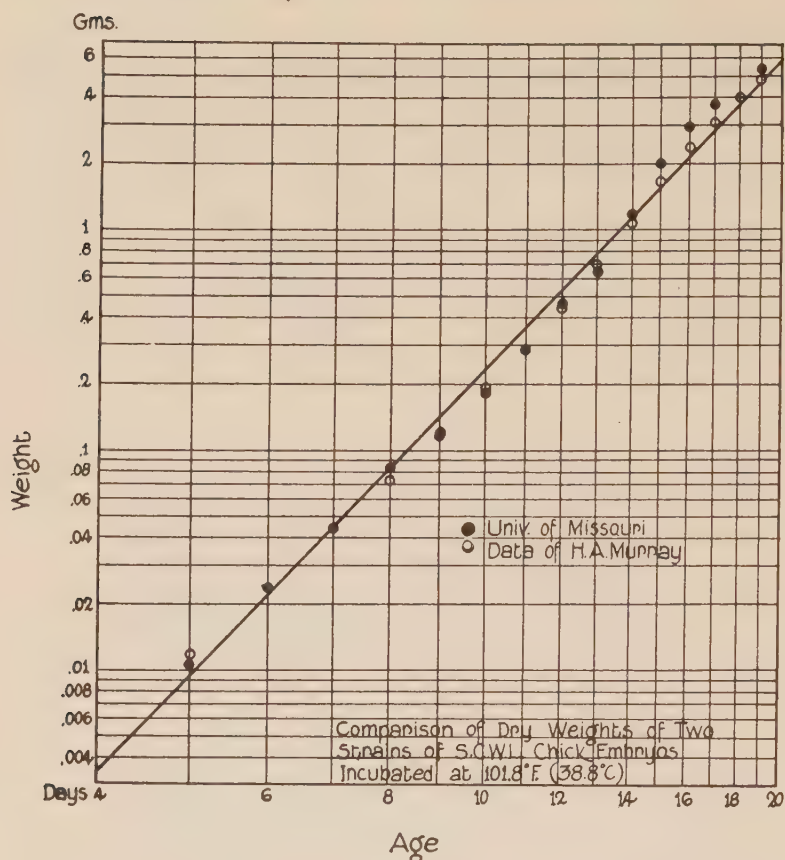


Fig. 3.—Murray's and Missouri data, dry weights, plotted on logarithmic coordinate paper. Note the peculiar but orderly deviations from the straight lines which were ignored by Murray, but which seem very significant to the present writer.

should therefore be used which emphasize the possible biologically significant deviations; and it is for this reason, in part, that the arithlog graph is used for comparative purposes in this work. Other reasons emphasizing the rational nature of the fit of this type of equation are given in Res. Bul. 97 of this series.

THE INFLUENCE OF TEMPERATURE

The influence of temperature upon growth is shown by charts, plotted from data in table 9. Figure 4 shows the cumulative growth for embryos incubated at various temperatures as measured by average

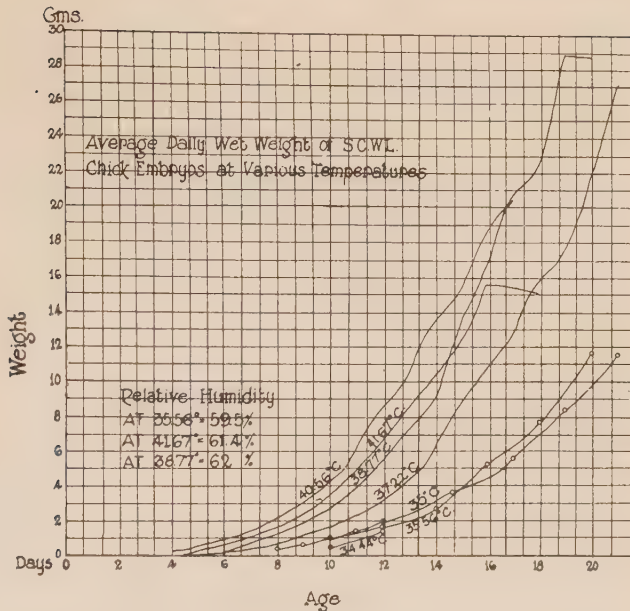


Fig. 4.—Influence of environmental temperature on the course of growth in wet weight of embryos.

daily wet weight. The data were obtained at the University of Missouri. Growth curves at 34.44 degrees 37.22 degrees and 40.56 degrees Centigrade are from data of Henderson (1924). They are included in the present work for comparative purposes. It is somewhat surprising that growth at 41.6°C. should be consistently less than growth at 40.5 degrees. It is also difficult to explain why growth at 35.5°C. is slightly lower than at 35°C. for a part of the first 15 days. It is possibly due to a lower room temperature which resulted in a lower actual temperature of the eggs, although the thermometer read 1°F. higher. Unfortunately, a record of room temperature was not kept in either case. A somewhat better comparison of growth at the different temperatures is shown by Fig. 5 where the data in table 9 are plotted on arithlog paper. The entire curves in all cases fail to approximate straight lines, therefore the exponential equation $W = Ae^{kt}$ will not fit throughout.

One of the primary reasons for obtaining these data was to ascertain if the influence of temperature upon the rate of growth of the chick embryo as measured by dry weight is similar to temperature influences upon other organisms such as plants, cold blooded animals and certain classes of chemical reactions. Such influences are shown by Kanitz (1915) and others to follow the generalization of Arrhenius and van't-Hoff, i. e.,

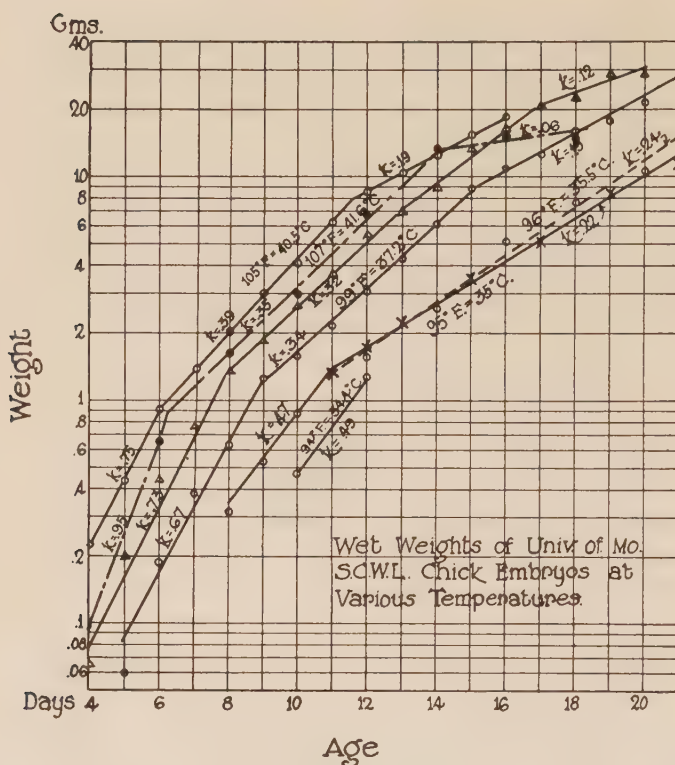


Fig. 5.—Influence of environmental temperature on the course of growth plotted on arithlog paper. Note the linear distribution of the data points for relatively enormous periods of the developmental cycle.

that for an increase in temperature of ten degrees Centigrade the speed of chemical reactions is doubled or more within certain limits. The value of this influence is usually expressed in the form of a temperature coefficient and designated Q_{10} . A method of calculating Q_{10} when the influence of temperature appears to be linear is shown by Henderson and Brody (1927) as follows:

$$Q_{10} = 1 - \frac{K_2 - K_1}{\frac{1}{2}(K_2 - K_1)} \times \frac{10}{(t_2 + t_1)} \quad (1)$$

where K_2 and K_1 are the instantaneous relative rates of growth at temperatures t_2 and t_1 respectively. This formula does not take into account the difference in the amount of growth which may have taken place prior to the time that weighing began. This growth can be accounted for if the time required to reach a given wet weight as determined from Fig. 5 is plotted against temperature as shown in Fig. 6. For the earlier stages

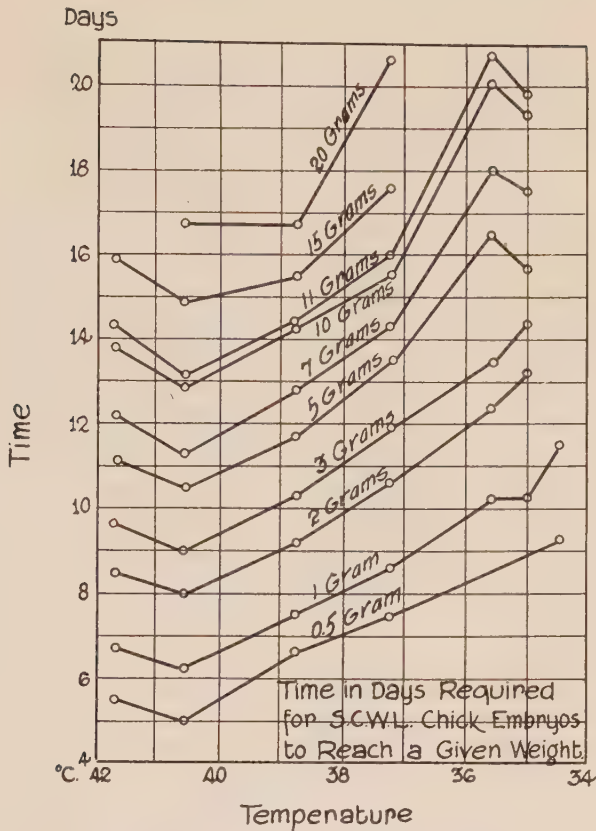


Fig. 6.—Influence of temperature on the time (in days) required to reach given wet weights.

of growth as e. g., wet weight 0.5 gram and 1.0 gram, the influence of temperature appears to be linear if weights near the lethal temperature value of 41.6 degrees C. are not considered. From a weight of 2 grams to 20 grams the curves appear to be nearly exponential in type. Since dry weight and nitrogen are to be the principal measures of growth in this work, wet weight will not be considered further. Figure 7 which is plotted from Figs. 8 and 9 shows clearly that the influence of temperature upon the time required to reach a given dry weight is not linear. Figure 10 shows the influence of temperature as measured by dry weight is approximately exponential since the values of time required to reach a given weight when plotted against temperature on arithlog paper give an approximation of a straight line. The fit is especially good for the time required to reach 1/10 gram in weight between the range of 40.5 degrees

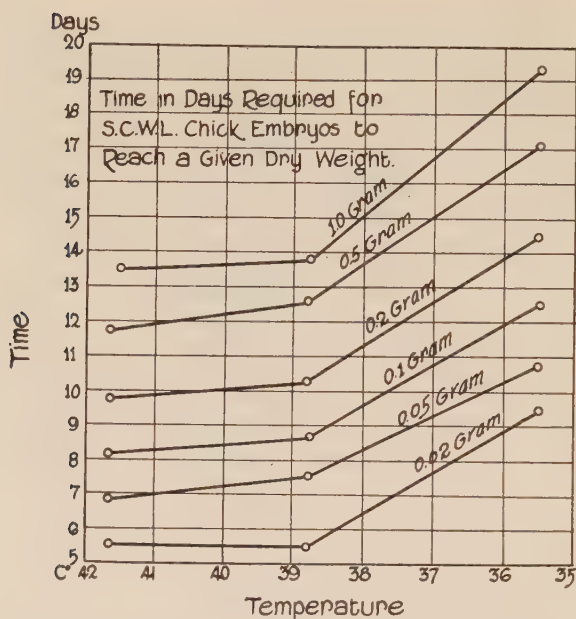


Fig. 7.—Influence of temperature on time (in days) required to reach given dry weights.

and 35.5 degrees. The temperature of 41.6 degrees is not considered since it is evidently so near the lethal value that it reduces the rate of growth. Since an interval of 10 degrees is used as a basis for evaluating temperature coefficients and since chick embryos probably cannot be grown to weighable size at limits as wide as 10°C. the growth between the limits of 40.5° and 35.5°C. must be used as a basis for estimating Q_{10} .

If the length of time to reach a given dry weight varies exponentially which it appears to do in Fig. 10, then to calculate temperature coefficient for an interval of ten degrees the lines which fit the data points between the limits of 35.5 degrees and 40.5 degrees may be extended to include an interval of 10 degrees or to 30.5 degrees. The quotient of the larger time value at 30.5 degrees over the time value at 40.5 degrees is Q_{10} since the time, T , required to reach a given weight is inversely proportional to the temperature.

$$Q_{10} = \frac{T_o}{T_{10}} \quad (2)$$

By this method the values for Q_{10} are calculated for the several weights as follows:

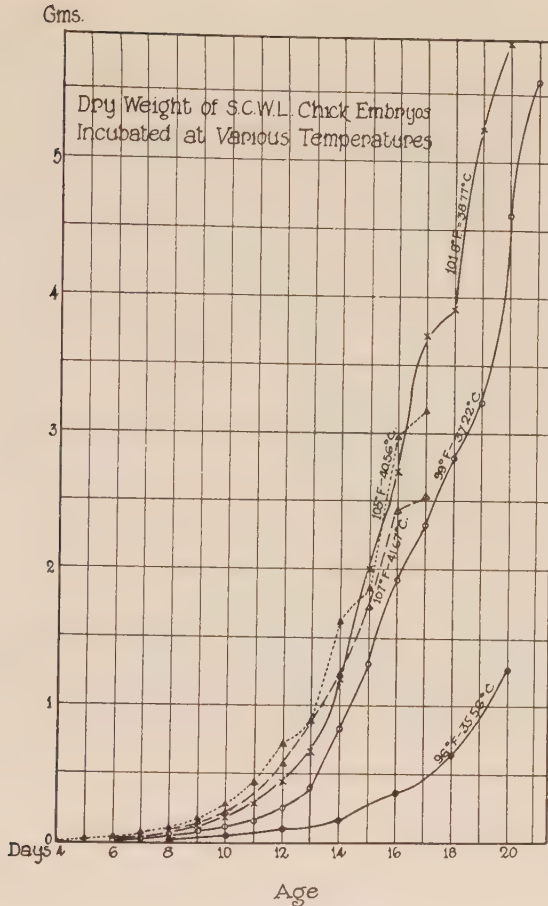


Fig. 8.—Influence of temperature on the course of growth in dry weight of chick embryos.

Weight in Grams	0.02	0.05	.010	.020	.050	1.0
Q ₁₀	3.2	2.5	2.2	2.3	2.2	2.1

It is doubtful whether this method is applicable in the case of the time required to reach one gram in weight since there is so much irregularity in the time required at different temperatures. In other words, the data points do not fall on a straight line. In view of the fact that the data points are necessarily partly determined by interpolation between intervals of 24 hours, the degree of fit is probably all that could be expected. In addition, attention should be called to the fact that the dry weights at 40.5 degrees are calculated from percentages determined at 41.6 degrees and not determined by difference between wet and dry weight.

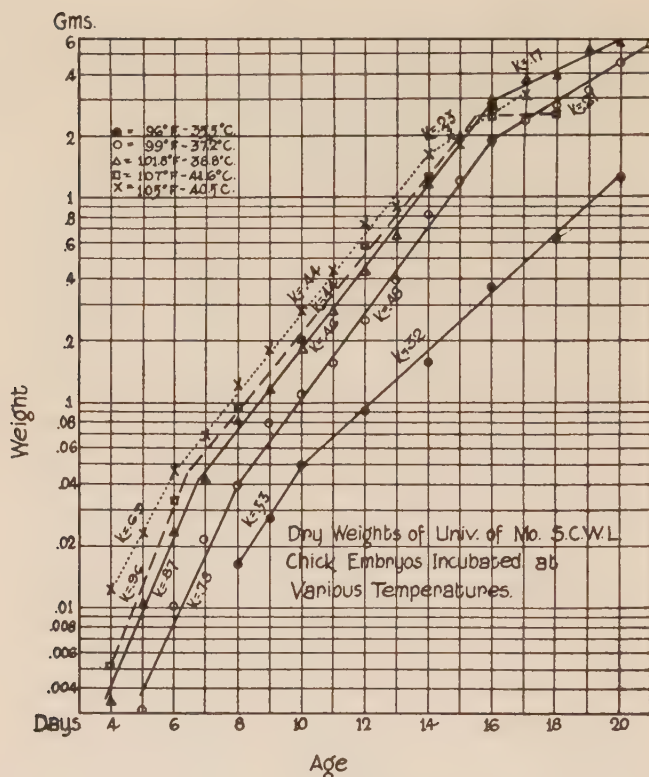


Fig. 9.—The dry weight data plotted on arithlog paper.

The temperature coefficient might be calculated by at least one other method although the amount of growth made prior to the time weighing began is not considered. This method makes use of the instantaneous percentage rates of growth at the different temperatures. If the influence of temperature is linear, formula (1) may be used. If the influence is exponential the following formula by Henderson and Brody (1927) could be applied.

$$Q_{10} = 1 - (\ln k_2 - \ln k_1) \times \frac{10}{t_2 - t_1} \quad (3)$$

Since a comparison of rates (as determined by the method which leaves out of consideration growth made between 0 and 4 days) did not demonstrate that the influence of temperature is either linear or exponential after the first stage, neither formula 1 nor 3 were used to calculate Q_{10} . It is apparent from Fig. 10 that there is little difference between

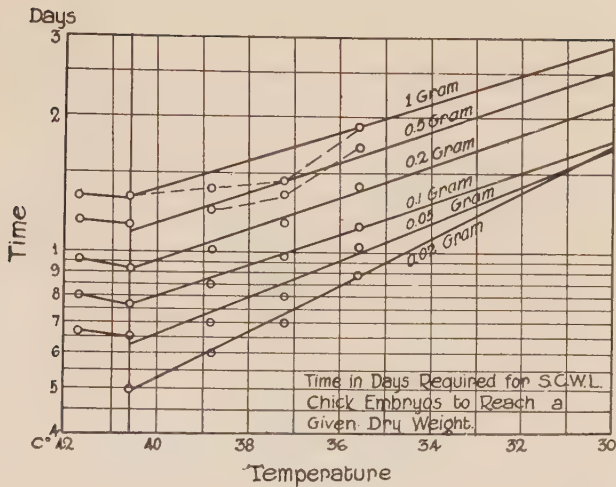


Fig. 10.—Time (in days) required to reach given dry weights.

the slopes of the curves (the k values) after a weight of about .05 grams is reached, except between the temperatures of 96° and 99°F. The instantaneous percentages rates ($100k$) at the various stages are indicated on the curves. These values are obtained from the formula

$$K = \frac{\log_e W_2 - \log_e W_1}{t_2 - t_1} \quad (4)$$

where W_2 is the weight at age t_2 and W_1 is the weight at age t_1

Nitrogen Content as a Measure of Growth

It seems reasonable that nitrogen should be the best measure of growth because it is probably the least variable and most important constituent of cell structure. Nitrogen content of Single Comb White Leghorn chick embryos incubated at 35.5, 38.8 and 41.6°C. are shown in Tables 1, 2, and 3. These data are plotted on arithlog paper as shown in Fig. 11. It is evident from this figure that there is little relative difference in the rate of growth except between the temperatures of 35.5 and 38.8. The fit of straight lines to the data points is not very good. The values at 35.5°C. are quite variable between the 14th and 16th day. There is no doubt an error in the amount of nitrogen determined on the 16th day since the percentage of the dry weight determined at this point is about 2 per cent greater than that for the 14th or 18th day. It is less probable that the error is in the dry weight. It is not probable that embryos actually contain less nitrogen on the 18th day at 41.6 degrees than they

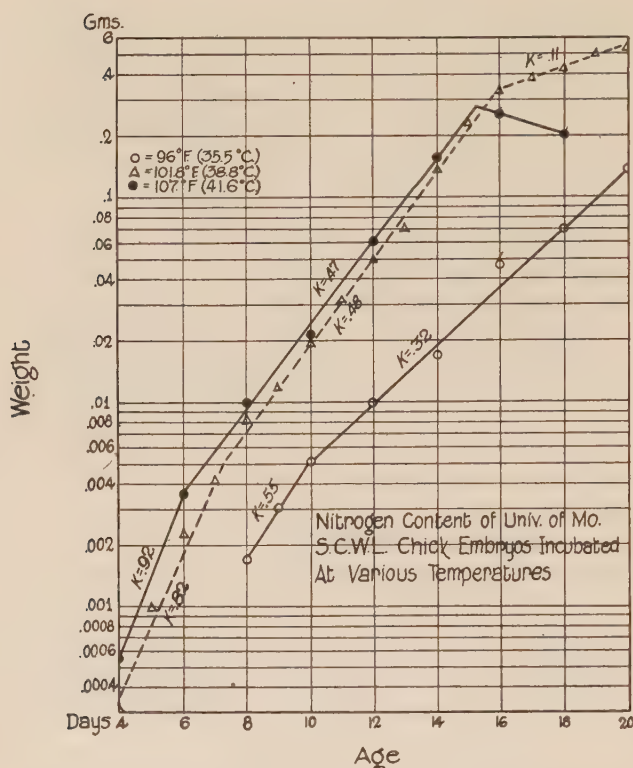


Fig. 11.—Data on influence of temperature on the course of growth in nitrogen plotted on arithlog paper.

do on the average on the 16th day. This variation as shown in the chart is no doubt due to the small number of embryos (2 in each case) from which the average was obtained. The temperature coefficients based on the time required to reach a given weight are calculated by formula (2) from Figure 7 and shown herewith. •

Weight in Grams	0.002	0.005	0.01	0.05	0.1
Q_{10}	2.2	2.2	1.9	1.7	1.8

The data points in Figs. 11 and 12 represent nitrogen determinations at the temperatures shown. It is possible to obtain more data points by calculating the nitrogen content of embryos grown at 37.2 degrees and 40.5 degrees in the same way that the dry weight was estimated, but probably little is to be gained from such interpretation. It is evident that different and higher values of Q_{10} can be obtained from the differences in time required to reach a given weight between the temperatures of 35.5 degrees and 38.8 degrees as indicated by dotted lines.

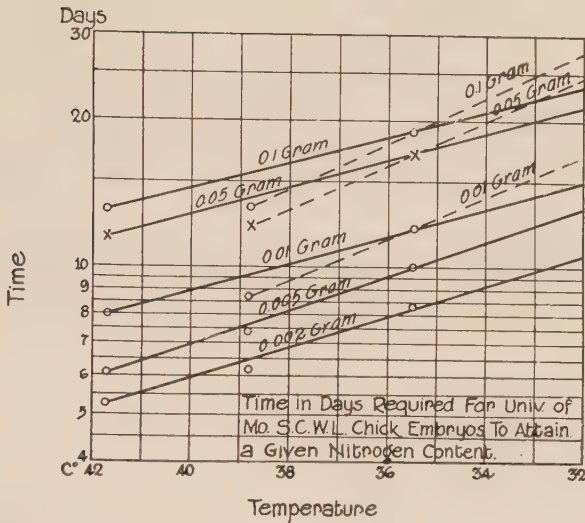


Fig. 12.—Influence of temperature on the time (in days) required to attain given body-nitrogen weights.

Limit of Temperature Influence

It is evident from the foregoing charts that the upper limit of temperature influence after the 15th day is between 38.8°C. and 40.5°C. since the growth rate as measured by time required to reach a given dry weight is reduced beyond the temperature of 38.8°C. Evidently the temperature regulating mechanism of the chick begins to function at about the 16th day. In other words, the chick embryo begins to react as a warm blooded animal at the age of 16 days or when it has reached a wet weight of approximately 20 grams or a dry weight of about 2 grams. The influence of temperature is apparently greatest during the earliest stages of growth. A comparison of the growth curves at 37.2 degrees and 38.8 degrees indicates that there is a difference in time required to reach a given weight of only one day, while the difference in time required to reach the given weight values between the temperatures of 37.2° and 35.5° steadily increases after a weight of about 0.05 grams is reached. In the first case a difference of about three degrees in temperature made only about one day's difference in the age of the embryos, and in the time required to hatch. Embryos at 38.8° were ready to hatch at about the 20th day while a few of those at 37.2° hatched during the 22nd day.

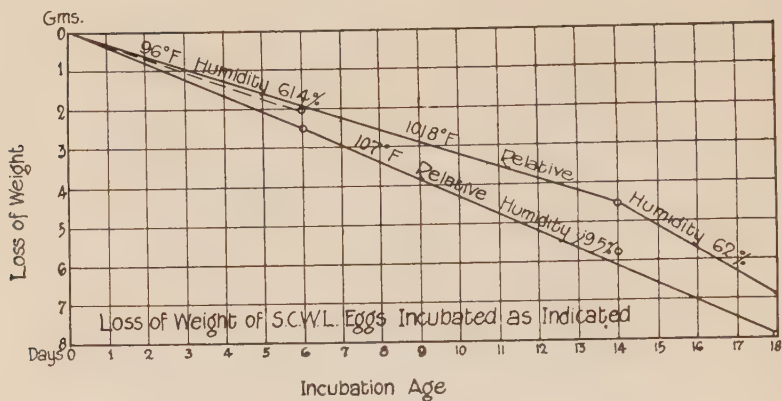


Fig. 13.—Weight losses in eggs during incubation.

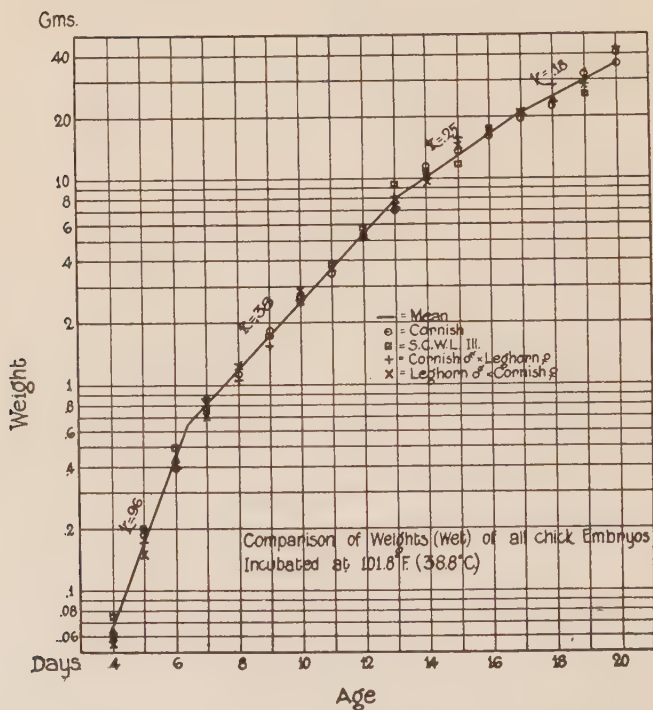


Fig. 14.—A comparison of the course of growth with respect to wet weights of all groups incubated at 101°F. (38.8°C.), plotted on arithlog paper.

Influence of Temperature on Embryo Mortality

In order to study the influence of temperature upon mortality one incubator was set with 200 eggs at 42.2°C and another at 35°C. In the first case all embryos were dead at the end of the 7th day. In the second case at 35°C. one chick hatched on the 28th day. This suggests the possibility of obtaining weight curves for short periods at limits slightly beyond the limits of 41.6° and 35° with a larger number of eggs in a larger machine.

While the ages at which the various embryos died was not determined at the different temperatures the total mortality at each temperature is shown in the following table.

SUMMARY OF INCUBATION RESULTS
WITH UNIVERSITY OF MISSOURI S. C. W. L.

Incubation conditions		No. eggs set.	Infertile		Dead Embryos		No. analyzed	
			Total	%	Total	%	Total	%
Temperature	107°F.	161	12	7.4	95	63	54	37
Humidity	59.5%							
Temperature	101.8							
Humidity	62. %	169	26	15	14	10	129	90
Temperature	96°F							
Humidity	61.4%	172	23	13	92	61	57	39

Influence of Temperature on Loss of Moisture of Eggs.

The loss of moisture from incubating eggs is seen to be slightly greater at the extremely high temperature of 41.6° as shown by Fig. 13. There is little difference in rate of moisture loss between the temperatures of 35.5°C. and 41.6°C. at practically the same average relative humidity. Loss of weight is seen to be almost directly proportional to time at all temperatures.

THE INFLUENCE OF BREED

In order to determine the influence of breed and strain upon the growth curve of the embryo, data were obtained from the University of Illinois strain of pure-bred White Leghorn and from pure-bred Dark Cornish of the same institution. Embryos produced by reciprocal cross matings of the two breeds were also grown and analyzed to determine any possible evidence of the influence of size and weight of parent stock or of hybrid vigor. In Fig. 14 the curves for the wet weights of embryos from the above described matings are shown. Figure 15 shows the dry

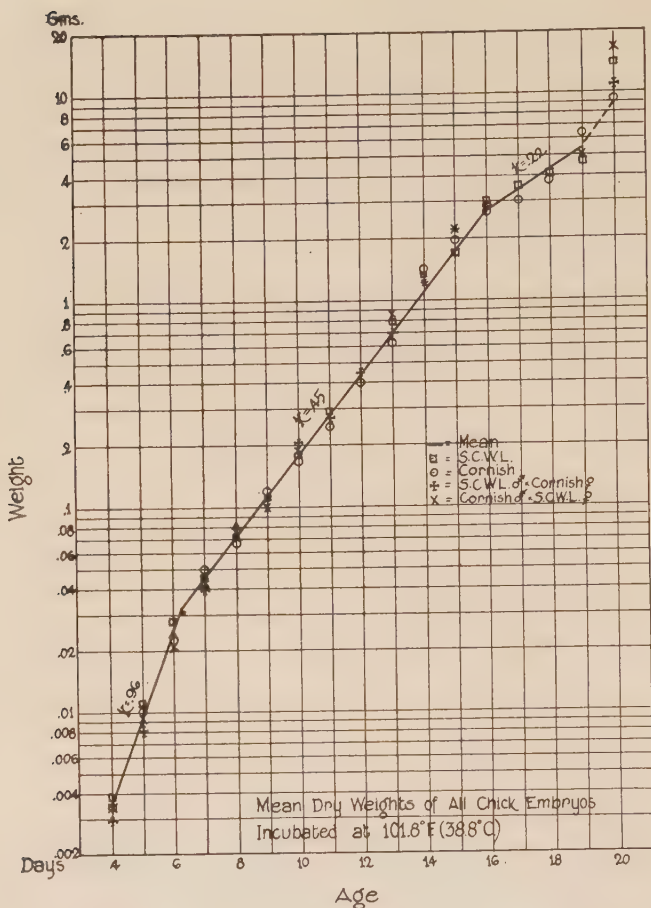


Fig. 15.—A comparison with respect to dry weights of all groups incubated at 101°F. Plotted on arithlog paper.

weights and Fig. 16 the nitrogen content. The Cornish and Leghorn embryos were incubated in the same machine at the same time. The cross-bred embryos were likewise incubated together in the same incubator but at a later period than the Leghorns and Cornish. Somewhat the same periods are evidenced as in case of the pure bred Leghorns previously discussed though the limits are different. In general, in the case of the average of the wet weights the periods seem to extend from the 4th to the 7th day, from the 7th to the 13th, and from the 13th to the 17th and from the 17th to the 19th day. These periods differ slightly from those shown when the dry weight and nitrogen content are taken as measures of growth as seen in Figs. 14 to 18. The mean of the weight

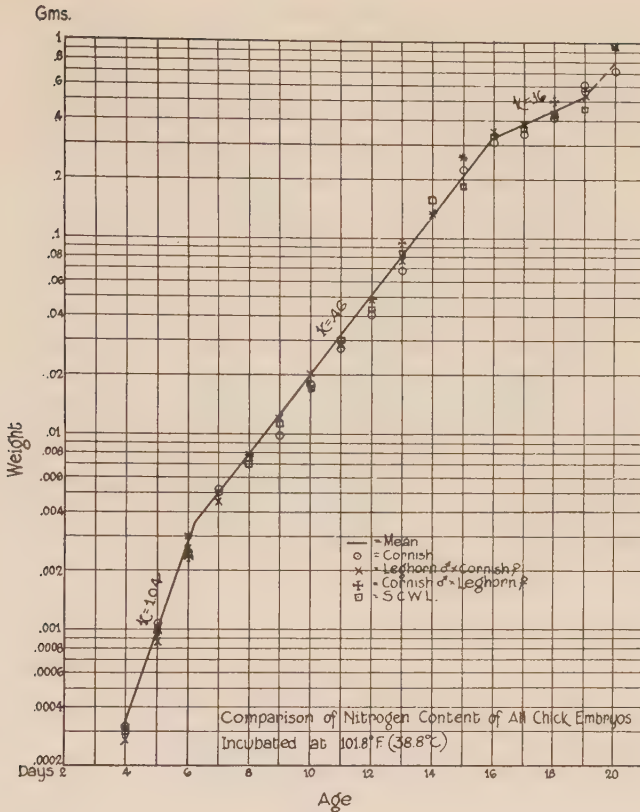


Fig. 16.—A comparison with respect to nitrogen weights of all groups incubated at 101°F. Plotted on arithlog paper.

curves for dry solid and nitrogen exhibit but three periods as illustrated in Fig. 17. The curves of the mean values as shown in the charts place the limits of the 2nd period at the 16th day. The slight difference between the classes of embryos may be the result of any one of several factors, or all combined. They may be the result of the breeding of the parent stock, or the incubation temperature may have actually been higher for the Illinois embryos because of the fact that there was less difference in temperature between the top and bottom of the egg, or it may be that the higher relative humidity increases growth especially between the 13th and 18th days. While the periods in these data do not coincide exactly with those obtained from the University of Missouri strain of White Leghorns, there is a close similarity between the two. The mean wet and dry weights and nitrogen content of all the embryos grown in

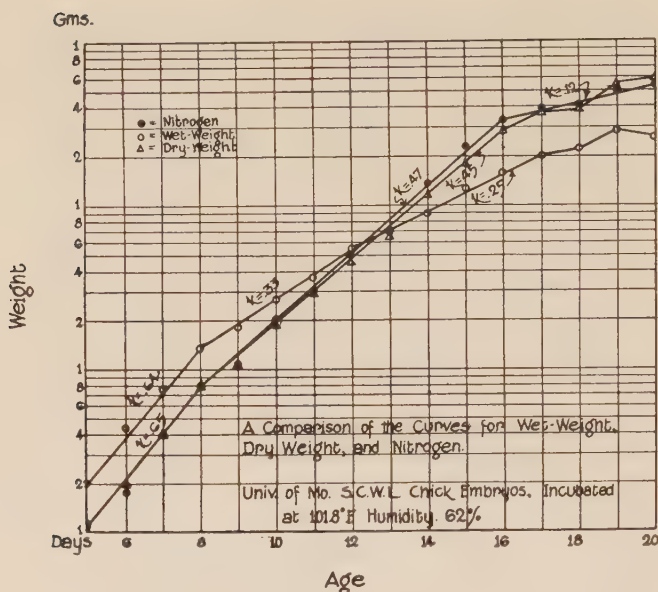


Fig. 17.—The dry weights, wet weights, and nitrogen weights plotted on the same arithlog grid.

this investigation at 101.8°F. at the University of Illinois and the University of Missouri are shown in Table 10 and Figs. 1, 3, 14, 15, 16, 17 and 18. In the foregoing charts the line represents the mean of the values of the different breeds and strains, which are indicated by legend. It seems evident from these charts that there is little difference in growth between the different breeds and strains of the embryos grown at a temperature of 101.8 degrees in this investigation. The embryos from the University of Illinois White Leghorns are consistently larger than the Cornish or the University of Missouri Leghorns up until the 7th day. This difference is not apparently consistent after this period. The Cornish embryos are consistently smaller than the mean until the 7th day after which time they do not differ materially from the others. The greater weight exhibited at the 20th day by the embryos grown at the University of Illinois is due to the fact that no attempt was made to squeeze out the yolk which had been absorbed into the body cavity, which was done in the case of the Leghorn embryos grown at the University of Missouri. The weight on the 20th day included the entire absorbed yolk in case of the Illinois chicks but not in the case of the Missouri chicks.

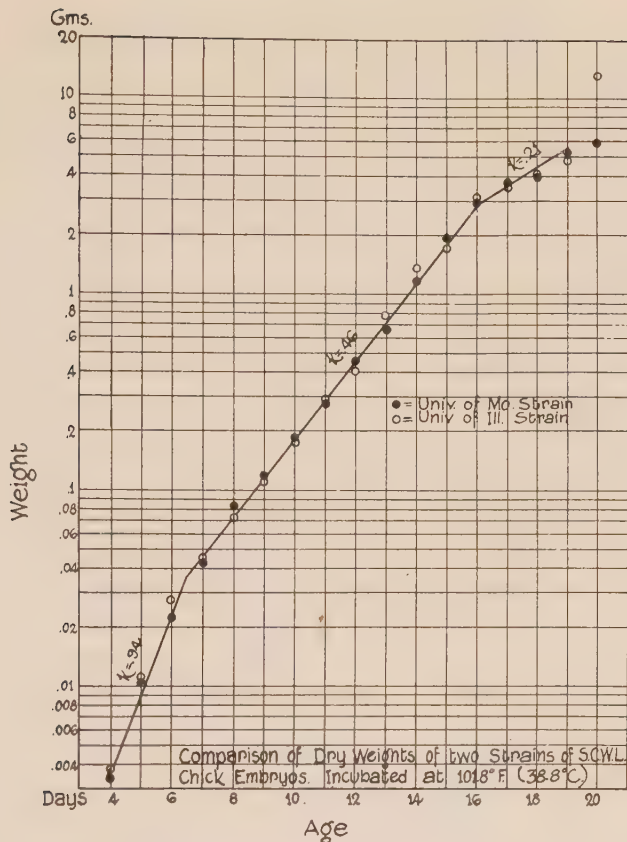


Fig. 18.—Data for two strains of White Leghorn chicks plotted on the same arithlog grid.

STAGES OF GROWTH

It has previously been noted that the compound interest type of formula, $W = Ae^{kt}$, seems to fit the growth curve of the chick embryo only for certain stages. When the logarithms of weight (either dry or wet or weight of nitrogen) are plotted against time on arithlog paper the resultant curves, at all temperatures, are not continuous straight lines, but a series of at least three straight lines. This would seem to indicate that there are stages or periods in the growth curve of the chick embryo during which the rate of growth is nearly constant. The changes in growth rate as shown by this method appear to be rather abrupt.

There is evidence that at least two other empirical curves can be used to represent the entire growth curve of the chick embryo, as measured by wet weight, somewhat better than the type of curve used to present

this data. Murray (1926), using the graphical method of curve fitting, shows that the curve represented by the formula $W = .668t^{3.6}$ will approximately fit the entire wet-weight curve of the chick embryos grown and weighed according to his technique. This indicates that the logarithm of weight is proportional to the logarithm of time. Schmalhausen (1926) shows that the cube root of the weight is approximately proportional to time. The temperature in his work varied from 40° to 38°C. from the first to the third week and the results are therefore not comparable to those of this investigation.

Murray (1926) used embryos of the same breed but of a different strain from those of this work, and obtained a slightly different wet-weight curve. A comparison of Murray's curve and the wet-weight curve obtained at approximately the same temperature in this investigation is seen in Fig. 1. Murray's values are somewhat lower for the most part than those obtained either for the University of Missouri White Leghorns or those of the University of Illinois. In all three sets of data a break in the curve is apparent between the 17th and 18th days. The temperature was probably about the same but the relative humidity in Murray's work was about 8% higher. Murray turned part of the eggs but once per day while all the eggs in this work were turned twice daily, which procedure conforms more nearly to accepted practice. Evidence has been presented that more frequent turnings influence hatching, but the writer is unaware of any data showing the influence an increased number of turnings per day has upon the growth of the embryo. There was probably some difference between the two methods of extracting embryos for weighing. Murray obtained a fairly smooth convex curve when his data were plotted on semi-arithlog paper but he obtained an approximation of a straight line when he plotted the logarithms of weight against the logarithms of time. He expressed the opinion that a break in the curve at the 17th day was a result of experimental error. While the wet weight is probably not as reliable as a measure of growth as the dry weight, or nitrogen content, it is rather interesting to note that several investigators using different procedure, obtain breaks in the growth curve of the chick embryo at approximately the same time as shown by Romanoff (1929). In a comparison of growth curves from widely different sources, Romanoff draws two conclusions. (1) "There are at least three well distinguished cycles in the growth of the fowls embryo." (2) "In general, the fluctuations in growth are not accidental and not the result of experimental error, but are oscillations caused by the normal chemical and physiological processes in the course of prenatal development."

Significance of Breaks in the Curve

In both sets of White Leghorn data obtained in this investigation, breaks in the wet weight curve occur at approximately the 7th, 13th, and 17th days as seen in Figs. 5, 14, and 17. Figure 17 suggests that these breaks in the wet weight curve are the result of a change in the water content of the embryos. The change in dry weight and nitrogen content is seen to occur at different periods. It is also evident from this graph that the water content of the embryos bears a rather constant relationship to the dry matter and nitrogen until about the 8th day when it changes rather abruptly. This change in relationship continues at a rather constant rate from this time until the 13th day and again at the 17th day. In Fig. 17 straight lines are drawn from the 5th to the 8th day, from the 8th to the 13th and from the 13th to the 17th. It is evident that the growth stages for different substances, i. e., wet weight and dry weight and nitrogen, are not exactly the same. The dry weight and nitrogen stages are practically the same, and they extend from the 5th to the 8th, from the 8th to the 16th, and from the 16th to the 20th day in the case of the nitrogen, but there is a very definite break in the dry weight line at the 17th day. Variations in temperature humidity, ventilation, and differences in breed and strain of parent stock can no doubt shift the limits of the growth periods of the embryo.

In general, for all strains and breeds of embryos grown in this investigation at 101.8°F. certain stages or periods of growth are evident. These stages vary somewhat depending upon what substance in the chick embryo is used as a measure of growth, but in general the limits of the periods are approximately between the 6th to the 8th and the 15th to the 17th days. The limits are probably more closely related to the attained weight of the embryo than to time, since the breaks occur at approximately the same weight whether the embryo be growing fast or slow as influenced by temperature.

Needham (1927) has shown that the chick embryo, during its development, uses successively three different types of chemical compounds as sources of energy. During the early period of development up to and including the 7th day he has presented evidence that carbohydrate is the source of energy. Between the 7th to approximately the 16th day protein is utilized and from the 16th day on, fat is combusted. It is interesting to note that the limits marking the changes in type of material utilized for energy by the chick embryo coincide roughly with the limits of the growth periods demonstrated in this investigation.

SUMMARY AND CONCLUSIONS

The results obtained in this investigation seem to support the following conclusions:

(1) Temperature exerts a profound influence on the growth rate of the chick embryo as measured by daily dry weight and nitrogen content and as indicated by temperature coefficients.

(2) This influence is greatest in the earliest stages of growth and it decreases at successive stages and practically ceases when the embryo is about 16 days old or when it has reached a dry weight of approximately 2 grams.

(3) During the earlier stages of growth the influence of temperature as shown by temperature coefficients follows the generalization of Arrhenius and van't Hoff.

(4) The temperature limits for growth to weighable size are approximately 34°C. and 42.2°C. in an average relative humidity of about 60 per cent.

(5) The temperature regulating mechanism of the chick is functioning at about the 16th day.

(6) Either three or four stages or periods of growth, during which the growth rate is fairly constant, are demonstrated at the temperature of 38.8 degrees Centigrade. The number and limit of the periods depends upon whether wet weight, dry weight or nitrogen are taken as a measure of growth.

(7) The limits of the periods are at the approximate ages of the fourth, sixth to eight, sixteenth to seventeenth, nineteenth to twenty-second days. There is evidence that an increase in temperature shortens the periods and shifts the limits.

(8) In general, the limits of the growth periods demonstrated in this investigation at 38.8 degrees coincide with the periods marking a change in the type of chemical compound utilized for energy.

(9) There is little if any constant significant difference in the growth of the embryos from the different strains and breeds used in this investigation.

(10) The percentage mortality was nearly the same at both extremes of temperature.

(11) Loss of moisture of eggs is slightly increased by an increase in temperature if the relative humidity is constant.

(12) Further studies are needed to establish optimum standard physical conditions for the development of the embryo.

REVIEW OF LITERATURE

The factors influencing growth and reproduction have, in varying degrees, occupied the attention of man for many centuries.

Knowledge of growth and reproductive processes is especially essential to the agricultural industry. As yet there are few data or few generalized laws for many of the fundamental growth processes of animals. The process of incubation, or growth of the chick embryo, with which many are casually familiar, is not completely understood from a physiological, chemical, or physical viewpoint. The morphology of the embryo has been extensively studied up to the stage when most of the adult organs can be identified. Beyond this stage morphologists as a class seem to find little which interests them.

Harvey (1651) is quoted by Lippincott (1927) as stating that "neither the schools of physicians, nor Aristotle's discerning brain, have yet disclosed how the hen and its seed doth mint and coin the chicken out of the egg". Lippincott (1927) further states that "this statement might be revised to include the great names in biological science, and the great schools of scientists, of the last centuries and yet be as true as when it was written." While this may hold true in relation to the correlation of details of the various steps in sequence, certainly more is known now about many of the various influences on embryonic development than was known in 1651.

In an attempt to discover a wide variety of possible influences upon the incubation and growth of the chick embryo the literature in Embryology and several related branches of science has been reviewed. The most important known influences upon embryonic development as measured by ability to hatch from the shell are classified as follows:

1. Parent stock
 - (a) Age
 - (b) Heredity
 - (c) Health and previous laying performance
2. Feed, care and management of parent stock and seasonal influences.
3. Selection, care and storage of eggs.
4. Hen vs. incubator
5. Incubator management
 - (a) Position and amount of turning of eggs
 - (b) Temperature
 - (c) Ventilation of egg chamber
 - (d) Relative humidity of air in the egg chamber.

Parent Stock

Hays (1928) presents evidence that "mature" birds both male and female tend to give higher hatchability than cockerels or pullets.

Stewart and Atwood (1909) found hatchability of two and three-year-old hens to be approximately 11% better than young "pullet fowls."

Pearl and Surface (1909) found hens were not superior to pullets in hatching power.

Pearl and Surface (1909) found "the character hatching quality of eggs as measured by the percent of fertile eggs hatched is definitely inherited in the female line, and probably also in the male line."

Hays and Sanborn (1924) find hatchability to be inherited and they indicate a gene (H) for hatchability.

Lamson and Card (1920) observed a strong correlation between the season's hatching percentage of hens and the hatching percentage of the same hens in successive hatches.

Jull (1929) shows that inbreeding tends to reduce hatchability. He concludes that "hatchability decreases as the coefficients of inbreeding increase."

Pearl and Surface (1910) show that crossing two breeds, Cornish and Barred Rocks, improves hatchability. Warren (1927) observed an increase in hatchability when Single Comb White Leghorns and Black Giants were crossed.

Sanctuary (1924) suggests that mal-positions of embryos prevent hatching and are probably inherited as a result of lethal genes. Hutt (1929) made similar observations and attributes fifty percent of embryo mortality to deformities.

Beaudette, Bushnell, and Payne (1923) found hens infected by *Bacterium pullorum* as indicated by reaction to the agglutination test, give a lower hatching percent than non-reacting hens.

Pearl and Surface (1909) found a positive correlation between high winter egg production and low hatchability the following spring. Lewis (1919) reports no relationship between the egg records of hens in the Vineland egg-laying contest and their hatchability.

Lamson and Card (1920) found no evidence of correlation between egg production and hatchability. Knox (1926) found rate and total production have a slight influence on hatchability. Kempster (1927) finds heavy breeds (American class) show a correlation of $+0.364 \pm 0.04$ between winter eggs and hatchability. No correlation between these variables was exhibited by Single Comb White Leghorns. Jull (1928) states "antecedent egg production at least for the four or five months preceding the hatching season, does not affect hatchability."

Feed Care and Management

One of the earliest reports of the influence of the ration on hatchability is that of Jackson and Cochel (1912). They state "hatchability of eggs and vigor are increased by a liberal use of corn in the ration." Whether yellow or white corn was not specified. Atwood (1914) found no difference in hatchability between hens on full rations and those on scanty rations. Buss (1920) observed little difference in hatchability between pens on various protein supplements such as meat scrap (in varying percentage), tankage and a combination of linseed meal and meat scrap. He noted that hatchability of hens on range was 65.6% of fertile eggs while that of hens confined indoors was 61.6%. Atwood (1922) reports hatchability of confined hens as 41.2% compared with 69.18% for hens allowed free range. In another case the same investigator found a difference in hatchability of approximately 10% in favor of hens permitted to range as compared to similar hens confined.

Halpin and Steenbock (1923) found that certain feeds deficient in vitamins influence hatchability. Eggs from hens on a diet of white corn and casein hatched 15.3% as compared to 23.6% for those fed yellow corn and casein. The addition of pork liver to a diet of yellow corn and casein increased hatchability to 62%. The same addition to a diet of a white corn and casein increased hatchability to 53%.

Payne and Hughes (1924) found that hens exposed to ultra violet rays ten minutes twice daily produced eggs which gave a hatchability of 75.6% whereas eggs from hens confined indoors and not exposed to ultra-violet rays gave a hatchability of 32.6%. Eggs from hens exposed to sunlight gave a percentage hatch of 58.4.

The Purdue Experiment Station (1925) reported no improvement in hatchability from feeding cod liver oil to layers. Payne and Hughes (1924) observed that when the ration was low in vitamins B and C the hatchability was 46%. When the ration

was low in vitamins A, D and C the hatchability of the pen was 17%. Holmes and co-workers (1925) found hatchability was materially increased by the addition of cod liver oil to the ration. Goodale (1926) found that cod liver oil and sprouted oats, and pig liver and sprouted oats fed to breeders which obtained sunlight through window glass did not give as good hatchability as the plan of allowing free range in sunlight.

Buckner, Martin and Peter (1925) found that restricting the calcium supply in a ration reduced hatchability. Kempster and Henderson (1925) observed indications that the kind of protein supplement used in rations for egg production influenced hatchability. The two vegetable proteins employed, cottonseed meal and soybean meal, gave low hatchability which was improved by the addition as a supplement, of 4% bone meal and 1% sodium chloride. Better hatchability was obtained from the pens receiving animal proteins than from the pens receiving supplemented vegetable proteins. In this test hatchability was 7% higher from the hens receiving dried buttermilk as a protein supplement. Kempster (1925) found hatchability was no better from pens receiving 1% cod liver oil in the mash than those which received sunlight through glass.

Penquite (1926) noted low hatchability when a large portion of the ration consisted of white corn. Hart and co-workers (1925) increased hatchability from 0 to 60% by irradiating the hens with ultra-violet rays. Irradiating the males only also improved hatchability. Hughes, Titus and Moore (1925) observed that hatching percentages of eggs from hens not exposed to ultra-violet light or sunlight were lower than others.

The Idaho Station (1926) found that cod liver oil was slightly better than lawn clippings as a source of vitamins. Both oil and clippings produced better hatchability than dry yeast or no supplement. Kempster (1927) noted that hatchability from pens exposed to winter sunshine was decidedly superior to those which were not so treated or to those which received cod liver oil alone as a supplement. Smith (1927) found little difference in hatching results between the following supplements buttermilk, germinated oats, alfalfa or cod liver oil, where the basal ration included 22% yellow corn meal.

Charles and Heywang (1927) obtained a slight improvement in hatchability by the use of ultra-violet light and cod liver oil. Atwood (1927) observed a slight improvement in hatchability when hens received a portion of the ration in the form of mash containing 20% meat scrap as a protein supplement, compared to hens which received whole grains only.

Kennard (1927) irradiated hens ten minutes daily with ultra-violet light and improved hatching results decidedly. In this comparison cod liver oil failed to improve hatchability. The addition of 4% bone ash and 4% fine oyster shells improved hatching results over the basically managed pen.

Wheeler (1929) reports decidedly poor fertility and hatchability where hens were deprived of direct sunlight throughout a winter feeding period previous to the time eggs were set in the spring. "Hens given access to open sunlight for several hours once every ten days and even at twenty-day intervals after the winter months and hens allowed free access to reflected sunlight after the same period with only filtered light were able to maintain good egg production throughout the laying season and to supply eggs from which a good percentage of strong chicks could be hatched."

From the foregoing it seems apparent that hatchability is influenced markedly by rations and management. Animal proteins as supplements apparently give better results than those of vegetable origin. Vitamins A and D (or its equivalent—ultra-violet rays) are certainly essential for good hatching results. Vitamins B and E are

no doubt essential but there are few projects reported to date which were designed to demonstrate the fact.

Selection, Care and Storage of Eggs

It has long been popular opinion that certain physical characteristics of hens' eggs such as size, shape, weight, specific gravity, or shell type, were related to hatchability. Experimental evidence on these points is meager and in general fails to support these theories.

Benjamin (1920) states "the size, the shape, and the color of the egg seem to have no effect on its incubation record." Crew (1922) did not determine any relation between the components of eggs and hatchability. Dunn (1922) found the percentage hatch of large eggs to be slightly lower than that of medium sized eggs. Mussehl and Halbersleben (1923) observed "little correlation between specific gravity, fertility, and hatchability of hen's eggs" also that "variations in the thickness of shell are more likely to influence specific gravity of eggs than are variations in protein or fat content." Jull and Haynes (1925) noted that "Egg shape where normal eggs are involved does not affect hatching quality." Also that "there is no significant correlation between the mean shape of eggs laid by an individual bird and the proportion of her fertile eggs which hatch." They observed also that egg weight had no bearing on hatching quality. Hays and Sumbardo (1927) found no relation between weight, length, diameter, specific gravity, and thickness and porosity of shell and shell membranes and hatchability.

In view of the foregoing it seems that the individuality of the parent stock should be the principal basis for selecting hatching eggs.

The influence of storage on hatching eggs seems to be largely a matter of time and temperature.

Edwards (1901) found that the lowest temperature at which eggs would develop was approximately 68 degrees F.

Mussehl and Bancroft (1924) state "our data indicate no lowering of the hatching power of hen's eggs after exposure to temperatures of 32 degrees F. for six hours. Exposure of eggs at 32 degrees F. for periods of 12-18 hours did not influence the hatching power to any marked degree." From present experimental evidence it appears that eggs should be stored in temperatures below 68 degrees F. and above freezing.

The length of time which eggs may be held in storage without injuring their hatchability as indicated by Waite (1919) is not over one week. He found deterioration was slight up to the sixth or seventh day after which it varies directly with age and that zero hatchability can be expected in twenty-eight days.

Comparison of Hens and Incubators

The relative efficiency of hens and incubators is still a debatable question. It is not uncommon for a hen to produce a hundred percent hatch and rather uncommon for an incubator to do likewise.

Chaddock (1925) records hen hatching to be 98% efficient as determined by thirteen hens.

Comparisons in hatching ability between hens and incubators made under comparable conditions are scarce. Observations on hen hatching necessarily cover a season of the year when conditions are more ideal for hatching since hens normally do not go broody until late spring.

The following comparison, while on a basis of total eggs hatched from total set, is interesting since it covers a long period of time and consequently a variety of conditions.

TABLE 1.—HENS VERSUS INCUBATORS
(Original data from J. P. Kenney, South Glastonbury, Conn.)

Year	Incubators			Hens		
	Eggs	Chicks	Percent hatch	Eggs	Chicks	Percent hatch
1901	743	322	43.2	340	182	53.5
1902	640	332	51.9	316	173	54.8
1903	680	307	45.1	388	242	62.4
1904	680	292	42.9	380	221	58.2
1905	200	107	53.5	468	283	60.5
1906	917	470	51.2	389	332	85.4
1907	776	441	56.8	541	333	61.6
1908	676	385	57.0	394	234	59.4
1909	434	277	63.8	407	280	68.8
1910	472	304	64.4	473	321	67.9
1911	724	400	55.2	540	298	78.0
1912	618	458	70.9	510	349	85.1
1913	606	427	70.5	558	380	68.1
1914	939	504	57.0	502	305	60.8
1915	597	294	49.4	360	259	71.9
1916	868	408	47.0	150	73	48.7
1917	505	280	55.4	182	113	62.1
1918	---	---	---	---	---	---
1919	502	347	69.1	102	38	37.2
1920	641	380	59.3	107	54	50.5
1921	789	468	59.3	195	90	46.2
Total	13007	7203	55.4	7302	4560	62.4

Note from Mr Kenney—January 16, 1922: "The first few years the incubator was run in the house cellar, the rest of the time in a 10x12 building. Began with one 100-egg Prairie State and used it for twenty years. Have had only one other make, that for a few years. Now have three Prairie States, two 140-egg with sand trays and one 220-egg with open bottom. The place where I run them is far from ideal, have to watch them like a cat does a mouse. The hens were set in lots of four to twelve at a time. The eggs were mostly my own, but have bought fifteen to one hundred outside most years. These in general hatched about as well as my own."

The following data were obtained from Mr. J. P. Kenney, South Glastonbury, Conn., and kindly loaned the writer by Dr. L. E. Card.

Comparison is made on the basis of percentage of total chicks hatched from total eggs set in incubators and under hens. The difference in hatching percentages on the above basis is not great, 55.4 for incubators vs. 62.4 for hens.

A question arises as to whether this difference is statistically significant.

Analysis of these data could be made as they stand without attempting to criticise the method of tabulation but it seems desirable that the two agencies should be compared directly in the same year rather than to compare one year for hens with another year for incubators which is being done in the above table if total percentages only are compared. In view of seasonal variations in this case, an average of the percentages of hatch for the twenty years should be better for comparison than the percentage hatch of the total. The mean percentage hatch is therefore calculated by the formula, the sum of annual percentages divided by twenty. The mean percentage hatch for incubators is 56.1% and for hens 62.09%.

In order to calculate the average deviation, standard deviation and probable error of the mean the data are rearranged in the following tables, 2 and 3.

TABLE 2

Year	% Hatch	Hens	
		d and fd	fd ²
1901	43.3	12.8	163.84
1902	57.9	4.2	17.64
1903	45.1	11.8	139.24
1904	42.9	13.2	174.24
1905	53.5	2.6	6.76
1906	51.2	4.9	24.1
1907	56.8	.7	.49
1908	57	.9	.81
1909	63.8	7.7	59.29
1910	64.4	8.3	68.89
1911	55.2	.9	.81
1912	70.9	14.8	219.04
1913	70.5	14.4	207.36
1914	57	.9	.81
1915	49.4	6.7	44.89
1916	47.0	9.1	82.81
1917	55.4	.7	.49
1919	69.1	13.0	169.00
1920	59.3	3.2	10.24
1921	59.3	3.2	10.24
Total		1123.0	1400.99
1123			70.05
20			
Standard Deviation			8.37
Em			±1.263

TABLE 3

Year	% Hatch	Incubators	
		d and fd	fd ²
1901	53.5	8.59	73.79
1902	54.8	7.29	53.14
1903	62.4	.31	.96
1904	58.2	3.89	15.13
1905	60.5	1.59	2.52
1906	85.4	23.31	543.35
1907	61.6	.49	.24
1908	59.4	2.69	7.23
1909	68.8	6.71	45.02
1910	67.9	5.81	33.75
1911	78.0	15.91	253.18
1912	85.1	23.01	529.46
1913	68.1	6.01	36.12
1914	60.8	1.29	1.66
1915	71.9	9.81	96.23
1916	48.7	13.39	179.30
1917	62.1	.01	
1919	37.2	24.89	619.51
1920	50.5	11.59	134.32
1921	46.2	15.89	252.49
Total		1241.91	2877.40
1241.91			
20			
Standard Deviation			11.974
Em			1.806

The mean percentage hatch from incubators is seen to be 56.1 ± 1.3 percent and from hens 62.1 ± 1.8 percent. The difference is 6 ± 2.2 percent. The difference over the probable error of the difference is 2.73. In order to be significant, the difference should be 3.8 times the probable error, therefore the difference of 6 percent cannot be considered significant.

Additional observations concerning the original data are as follows:

1. Hens no doubt became broody late in the spring when eggs were of better quality than those set in incubators earlier the same year.

2. Percent hatch is on a basis of total chicks hatched from total eggs set which does not take infertile eggs into account, though it might be assumed the percentage infertile was approximately the same for both agencies if hens and incubators were set at the same time. It is well known, however, that fertility improves as the hatching season progresses and this would again give hens the advantage. ♀

CORRECTION

Caption of Table 2 should read "Incubators";
of Table 3 "Hens" Third figure in last column
of Table 3 should read .096

Incubator Management

Early investigations relative to the influence of temperature upon hatchability probably did not take other influences into consideration to a great extent since influences such as genetic or nutritional had not been studied prior to 1900. In fact prior to 1900, temperature alone seems to have been regarded as about the only factor aside from turning, although Dareste (1886), according to Lippincott (1927) "reports that eggs in a vertical position developed normally, if the large end were up, and abnormally when it was down."

Graham (1903) in a trial with 120 eggs found that those laid on their sides hatched better than those placed on either end.

Eycleshymer (1907) states that "the position of egg is a factor of little importance." Jackson (1912) found no serious disadvantage from standing eggs on end for three days but he states "eggs laid flat and turned twice daily gave better results than those kept in any other position."

Turning

Turning has long been known to be a necessary procedure in artificial incubation. Just how much turning may be necessary or how long it should continue is not definitely known. Eycleshymer, (1907), who seems to be one of the first to report the effect on hatchability when eggs were not moved during incubation, found this treatment gave a 15% hatch, compared with a hatching percent of 45% for those turned twice daily and 58% for those turned five times daily. Payne (1921) observed that turning four to six times per day gave better hatching results than turning six times especially in the early season when there was an average difference in temperature of the air of the egg chamber of six degrees F. between the top and bottom of the egg. Payne (1921) also found that the hen in natural incubation turns the eggs at least once per hour.

Chattock (1925) found that turning eggs five times daily gave approximately 11% better hatches than eggs turned twice, and as good results as eggs turned eight times. He found turning forty-eight times per day by motor-driven tapes was decidedly detrimental which he suggests was due to vibrations of the motor. Card (1926) observed that eggs not turned hatched poorly while those turned twice daily for the first six days hatched nearly as well as those turned twice daily throughout the incubation period.

Temperature

According to Lippincott (1927), who cites Harvey (1651), von Baer (1828), and Kellicott (1913), a temperature of 100.4 degrees F. is given as the optimum for development of the embryo while Dareste (1891) according to the same writer, stated normal development occurred in a temperature range of 95 degrees to 102 degrees F. The recommendations of incubator manufacturers vary from 99 degrees to 103-104 degrees F. based no doubt upon hatching results obtained in private trials. It is becoming increasingly evident that the temperature of the egg chamber alone cannot be accepted as the controlling factor unless other conditions such as method of heating, ventilation and humidity are known, including temperature of the room in which the incubator is operated. Payne (1921) found an average difference in temperature of air in the egg chamber of as much as 6 degrees F. between the top and bottom of the eggs in early season when the temperature of the room in which the incubator was operated was low. This difference seemed to disappear later in the season when the room temperature was increased to 85 degrees F. The writer (1924) noted a difference in temperature of as much as 2.8 degrees F. between the stratum of air on a level with the top of the egg and that at the bottom of the egg in a Prairie State Hot Air Incubator operated in a room which was approximately

70 degrees F. Unfortunately, the actual temperature of the eggs was not determined in either case.

Eycleshymer (1907) determined the relation between the temperatures of hens and that of the eggs under the hens. He found an initial difference at the beginning of the hatching period of 4.2 degrees F. decreasing to 1.6 degrees F. on the twentieth day. Similar tests with incubators gave an initial difference of 2.8 degrees F. the first day and 1 degree F. on the twentieth day. Other influences may operate to vary the difference in actual temperature of the egg and the egg chamber and also the differences between strata of air in the egg chamber. Such influences may be rapidity and direction of air circulation, temperature of the air passing into the machine, and relative humidity. In so-called forced draft incubators, the air is driven rapidly by fans or reels and a fairly uniform temperature is maintained at all levels. Such machines are recommended to be operated at temperatures as much as four degrees lower than the small "farm" type incubators in which the air is circulated by convection. There is no doubt an optimum temperature for a given set of conditions which seems to be within the range of 99 degrees to 104 degrees F. In contrast to the conditions considered ideal for forced draft mammoths, which provide a uniform degree of temperature between the top and bottom of the egg is the suggestion of Atkinson (1924) that the difference of from 14 degrees to 18 degrees between the top and bottom of the eggs under hens as determined by Cadman (1923) is "the missing factor in artificial incubation." According to Atkinson (1924) this temperature difference under hens when reproduced by a mechanical incubator improved hatchability from an average of 55% to 89% of all eggs set. Unfortunately other factors such as the age, breed, and management of the hens are not given in Atkinson's paper. Philips and Brooks (1923) came to the conclusion that the optimum temperature of the egg chamber for hatching in a Prairie State Hot air incubator was 101 degrees throughout the incubation period.

Ventilation

The need of the embryo for oxygen seems obvious and the experimental proof has recently been reviewed by Lippincott (1927) and is therefore omitted here. The carbon dioxide produced as a measure of respiration has been studied by Pembrey, Gordon, and Warren (1894-5), Bohr and Hasselbalch (1900), Lamson and Edmond (1914), Atwood and Weakley (1924)), and Murray (1926). Lamson and Edmond (1914) found that hatchability was not reduced if the carbon dioxide content of the air in the incubator did not exceed 150 parts in 10,000. They obtained relatively good hatches (above 65%) when the carbon dioxide content of the air was slightly in excess of 200 parts in 10,000. Chattock (1925) compared the ventilation in the hen's nest with incubators and concluded that the ventilation in the incubators was ample since it exceeded that of the hen's nest.

Relative Humidity

The importance of a high degree of relative humidity in the egg chamber has only recently come to be generally recognized by incubator manufacturers. According to Lippincott (1927) the need for moisture in incubation was proved by Baudrimont and St. Ange as early as 1847. Dryden (1907, 1908) and Graham and Day (1908) demonstrated that increasing the relative humidity in incubators by the use of moisture pans increased the hatch. Dryden (1908) found a relative humidity of 55% gave better results than 48% or 64%.

Murray (1925) in a study of the influence of relative humidity of the egg chamber upon the rate of evaporation of moisture from the egg found the rate of evaporation in a relative humidity of 90% was approximately 2% for an eighteen-day period, 7%

when the relative humidity was 65%, and 15% when the relative humidity was 23.5%. Eycleshymer (1907) noted a 15% loss of moisture from eggs under hens.

Townsend (1929) found that with a relative humidity of approximately 32% in a mammoth incubator with forced air circulation eggs lost 17.4% in weight in eighteen days. An increase in relative humidity to between 56% and 57% reduced the loss in weight to 10.5%.

While there is variation in the findings of the various investigators, it appears that if the relative humidity is kept within a range of 40% to 75% hatchability is not materially affected.

In general, the influences upon growth of the chick embryo as measured by the percentage of chicks which hatch appear to be of two classes: (1) Influences on egg quality; (2) physical influences controlled by the incubator.

Influences in neither group can be regarded as standardized on a plane with certain chemical or physical laws.

While the percentage of chicks which hatch is the logical and practical measure of success a study of the development of the embryo throughout the incubation period is probably essential to a solution of the problem of hatchability. The morphology of the embryo throughout the incubation period has been studied by Duval (1889) and Lillie (1919). Various quantitative measures of development have been made by different investigators. Hasselbalch (1900) obtained the wet weights of embryos for each successive day from the third to the eighteenth day. Lamson and Edmond (1914) made similar weighings from the fourth to the twentieth day. Henderson (1924) obtained data on the wet weights of embryos at varying temperatures and approached the limits of temperature for development to weighable size and found a marked acceleration of the growth rate followed an increase of temperature. In this respect the chick embryo appeared to follow the Arrhenius-von't Hoff law. Mitchell, Hamilton, and Card (1925) obtained wet and dry weights of embryos from the fifth to the twenty-first day.

Murray (1926) obtained daily weights of embryos from the fifth to the nineteenth day and made analyses for protein, fat, ash, and glycogen. Schmalhausen (1926) studied the weight and dimensions of various organs at successive ages.

While results differ, the difference is perhaps no greater than could be expected under different conditions. Some of the possible causes for lack of complete agreement of results in such studies as those mentioned above may be, variations in incubation methods, variations in technique of extracting embryos, variations in breed of parent stock. A knowledge of the limits of various influences is essential if standards are to be established.

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VITA

Earl Wilton Henderson was born May twenty-ninth, 1894, on a farm near Carlyle, Illinois. He is a son of Justin Mortimer Henderson and Emma Florence (Wilton) Henderson.

He attended Clinton and St. Clair County (Illinois) public schools; Ralph Sellew Institute (Y.M.C.A.); and the University School, St. Louis, Missouri. He entered the College of Agriculture of the University of Missouri in September, 1915. In May, 1917, he entered the fourteenth provisional training regiment of the United States Army at Fort Riley, Kansas, and was commissioned a provisional second Lieutenant of cavalry in the Regular Army in August, 1917. He was promoted to first lieutenant in October, 1917, and served with the Seventh Division in the American Expeditionary Forces. He resigned his commission and was honorably discharged from the army in June, 1919. He reentered the College of Agriculture of the University of Missouri in June, 1919, and graduated with the degree of Bachelor of Science in Agriculture, 1921. He was appointed instructor in poultry husbandry in the College of Agriculture of the University of Missouri in 1921, and entered the graduate school of that institution the same year. He was promoted to assistant professor in 1922. In 1924 he was awarded the degree of Master of Arts by the University of Missouri. He attended the Graduate School of the University of Wisconsin the summer of 1927, and the Graduate School of the University of Illinois, 1927-28 and the summer of 1929.

In February 1930 he was appointed professor of poultry husbandry at Iowa State College.

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He married Esther Louise Logan in February 1918 and they have two children, Philip Hahn and Wilton Logan Henderson.

He is co-author of the following publications:

The Rate of Senescence of the Domestic Fowl as Measured by the Decline in Egg Production With Age. *Journ. Gen. Physiol.* VI, 1:41-45. 1923.

The Effect of Temperature on the Percentage-Rate of Growth of the Chick Embryo. *Missouri Agr. Exp. Sta. Res. Bul.* 99, 1927.

